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ORIGINAL PAPER

Science, evolution and natural selection: in praise of Darwin at the Stazione Zoologica Anton Dohrn of Naples

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Abstract Copernicus, Galileo, Newton and other physical scientists ushered in a conception of the universe as matter in motion governed by natural laws. Their discoveries brought about a fundamental revolution, namely a commitment to the postulate that the universe obeys immanent laws that can account for natural phenomena. The workings of the universe were brought into the realm of science: explanation through natural laws. Darwin completed the Copernican revolution by extending it to the living world. Darwin demonstrated the evolution of organisms. More important yet is that he discovered natural selection, the process that explains the 'design' of organisms. The adaptations and diversity of organisms, the origin of novel and complex species, even the origin of mankind, could now be explained by an orderly process of change governed by natural laws. The origin of species and the exquisite features of organisms had previously been explained as special creations of an omniscient God. Darwin brought them into the domain of science.

Keywords Christiane Groeben · Scientific revolution · Adaptation · Natural theology · Fossil record · Molecular evolution

In this essay I have made extensive use of a paper presented on 3 March 2009 at the International Conference, *Biological Evolution Facts and Theories. A Critical Appraisal 150 Years After The Origin of Species*, Pontifical Gregorian University, Rome 3–7 March 2009; and previous publications of mine: "One hundred fifty years without Darwin are enough!", *Genome Research,* 19, 2009:693–699; "Where is Darwin two hundred years later?", *Journal of Genetics,* 87, 2008:321–325; "Evolution in the 21st Century" In: Kleinman D., Delborne J., Cloud-Hansen K., Handelsman J. (eds.), *Controversies in Science & Technology*, vol. 3: From Evolution to Energy, New Rochelle: Mary Ann Liebert Inc., 2010, 79–90; and *Darwin's Gift to Science and Religion*, Washington, DC: Joseph Henry Press, 2007.

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I have known Christiane Groeben and considered her a friend for more than three decades. Our relationship has, through all these years, been associated with the Stazione Zoologica Anton Dohrn of Naples. Starting in the 1970s, I was occasionally, mostly in the summer, a seminar or lecture speaker in the main research and conference building at the Aquarium in Naples' magnificent Bay, but also often at the Stazione's lovely 'tower' on the island of Ischia. In 1982, a public symposium was held at the magnificent Castel Dell'Ovo in the Bay of Naples to commemorate the 100th anniversary of Darwin's death. A large number of chairs and a podium with a microphone had been set in a large hall at the castle. Among the speakers were the eminent evolutionists Ernst Mayr and Stephen Jay Gould. Their lectures were spoken or read. I had announced that I would use slides for my lecture and a projector had been set up with a huge whitened wall serving as the screen. When the time for my lecture arrived, I noted with distress that no pointer was available. Instantly, Christiane was ready for a solution. Just as I was starting to speak she came to the podium with an incredibly long-stem rose that she had observed at a tourist stand near the entrance to the castle. I was amused, thrilled, and thankful.

Over the years, my interactions with Christiane would be related to the Stazione's library and the journal, *History and Philosophy of the Life Sciences*, but my visits always included a lecture or seminar. From time to time, when suitable, Christiane would bring a long-stem rose for me to use as a pointer, as a lovely and amusing memory of my lecture at the Darwin centenary symposium. Each time, as in 1982, I thought of Richard Strauss' *Der Rosenkavalier*. Christiane Groeben was and still is for me 'The Dame of the Rose'. I offer, with joy and honor, the reflections about Darwin that follow as a tribute to Christiane Groeben's long time dedication and excellence at the Stazione Anton Dohrn.

1 Darwin in the history of ideas

Charles Darwin was born in 1809, published *On the Origin of Species* in 1859, and died in 1882. The 100th, sesquicentennial, and 200th anniversaries of those 2 years were celebrated in universities, natural history museums and other institutions throughout the world with scientific lectures, symposia, exhibitions, and otherwise.

Darwin occupies an exalted place in the history of Western thought, deservedly receiving credit for the theory of evolution. In *On the Origin of Species*, he laid out the evidence demonstrating the evolution of organisms. Darwin characteristically did not use the term 'evolution', which did not have its current meaning, but referred to the evolution of organisms by the phrase "common descent with modification" and similar expressions. However, Darwin accomplished something much more important for intellectual history than demonstrating evolution. Indeed, accumulating evidence for common descent with diversification may very well have been a subsidiary objective of Darwin's masterpiece. Darwin's *Origin* is, first and foremost, a sustained argument to solve the problem of how to account scientifically for the design and diversity of organisms. Darwin seeks to explain the adaptations of organisms, their complexity, diversity, and marvelous contrivances as the result of natural processes. Darwin brings about the evidence for evolution because evolution is a necessary consequence of his theory of natural selection that accounts for the adaptations of organisms and their diversity.

There is a version of the history of the ideas that sees a parallel between the Copernican and the Darwinian revolutions. In this view, the Copernican Revolution consisted in displacing the Earth from its previously accepted locus as the center of the universe, moving it to a subordinate place as just one more planet revolving around the sun. In congruous manner, the Darwinian Revolution is viewed as consisting of the displacement of humans from their exalted position as the center of life on earth, with all other species created for the service of humankind. According to this version of intellectual history, Copernicus had accomplished his revolution with the heliocentric theory of the solar system. Darwin's achievement emerged from his theory of organic evolution.[1]

I propose that this version of the two revolutions is inadequate: what it says is true, but it misses what is most important about these two intellectual revolutions, namely that they ushered in the beginning of science in the modern sense of the word. These two revolutions may jointly be seen as one scientific revolution, with two stages, the Copernican and the Darwinian. Darwin is deservedly given credit for the theory of biological evolution, because he accumulated evidence demonstrating that organisms evolve and discovered the process, natural selection, by which they evolve their functional organization. But Darwin's *Origin* is most important because it completed the Copernican Revolution, initiated three centuries earlier, and thereby radically changed our conception of the universe and the place of mankind in it.

The Copernican Revolution was launched with the publication in 1543, the year of Nicolaus Copernicus' death, of his *De revolutionibus orbium celestium* (*On the Revolutions of the Celestial Spheres*), and bloomed with the publication in 1687 of Isaac Newton's *Philosophiae naturalis principia mathematica* (*The Mathematical Principles of Natural Philosophy*). The discoveries of Copernicus, Kepler, Galileo, Newton, and others, in the sixteenth and seventeenth centuries, had gradually ushered in a conception of the universe as matter in motion governed by natural laws. It was shown that the Earth is not the centre of the universe, but a small planet rotating around an average star; that the Universe is immense in space and in time; and that the motions of the planets around the Sun can be explained by the same simple laws that account for the motion of physical objects on our planet; laws such

[1] Sigmund Freud referred to these two revolutions as 'outrages' inflicted upon humankind's self-image and adds a third one, his own: ''Humanity in the course of time had to endure from the hands of science two great outrages upon its naïve self-love. The first was when it realized that our earth was not the centre of the universe, but only a tiny speck in a world-system of a magnitude hardly conceivable; this is associated in our minds with the name of Copernicus, although Alexandrian doctrines taught something very similar. The second was when biological research robbed man of his peculiar privilege of having been specially created, and relegated him to a descent from the animal world, implying an ineradicable animal nature in him: this transvaluation has been accomplished in our own time upon the instigation of Charles Darwin, Wallace, and their predecessors, and not without the most violent opposition from their contemporaries. The third and most bitter blow upon man's craving for grandiosity" was meted out in the twentieth century by psychoanalysis, revealing that man's *ego* "is not even master in his own house" (Freud 1993 [1920], p. 562).

as $f = m \times a$ (force = mass × acceleration), or the inverse-square law of attraction, $f = g(m1 \times m2)/r^2$ (the force of attraction between two bodies is directly proportional to the product of their masses, but inversely related to the square of the distance between them). These and other discoveries greatly expanded human knowledge, but the conceptual revolution they brought about was more fundamental yet: a commitment to the postulate that the universe obeys immanent laws that account for natural phenomena. The workings of the universe were brought into the realm of science: explanation through natural laws. Physical phenomena could be accounted for whenever the causes were adequately known.

Darwin completed the Copernican Revolution by drawing out for biology the ultimate conclusion of the notion of nature as a lawful system of matter in motion. The adaptations and diversity of organisms, the origin of novel and highly organized forms, the origin of mankind itself, could now be explained by an orderly process of change governed by natural laws.

2 From natural theology to natural selection

The advances of physical science had driven mankind's conception of the universe to a sort of intellectual schizophrenia, which persisted well into the mid nineteenth century. Scientific explanations, derived from natural laws, dominated the world of non living matter, on the Earth as well as in the heavens. However, supernatural explanations, depending on the unfathomable deeds of the Creator, were accepted in order to account for the origin and configuration of living creatures—the most diversified, complex, and interesting realities of the world. It was Darwin's genius that he resolved this intellectual inconsistency. Darwin completed the Copernican Revolution by bringing the design of organisms into the realm of science, as an outcome of natural processes governed by natural laws.

The conundrum faced by Darwin can hardly be overestimated. The strength of the 'argument from design' to demonstrate the role of the Creator had been forcefully set forth by the English clergyman and author William Paley in his *Natural theology; or, Evidences of the existence and attributes of the deity*, published in 1802, a book that had greatly impressed Darwin, while he was a student at Cambridge University. *Natural theology* is a sustained argument-from-design claiming that the living world provides compelling evidence of being designed by an omniscient and omnipotent Creator. Paley's keystone claim is that, "There cannot be design without a designer; contrivance, without a contriver; order, without choice; means suitable to an end, and executing their office in accomplishing that end, without the end ever having been contemplated" (Paley 1802, pp. 15–16).

The argument-from-design to demonstrate the existence of God had been put forward by theologians and other authors over the centuries. But Paley elaborated the argument-from-design with greater cogency and more extensive knowledge of biological detail than has ever been done by any other author, before or since. Paley brings in all sorts of biological knowledge, from the geographic distribution of species to the interactions between predators and their prey, the interactions between the sexes, the camel's stomach and the woodpecker's tongue, the compound eyes of insects and the spider's web. *Natural theology* has chapters dedicated to the complex design of the human eye; to the human frame, which displays a precise mechanical arrangement of bones, cartilage, and joints; to the circulation of the blood and the disposition of blood vessels; to the comparative anatomy of humans and animals; to the digestive system, kidneys, urethras, and bladder; to the wings of birds and the fins of fish; and much more. After detailing the precise organization and exquisite functionality of each biological object or process, Paley draws again and again the same conclusion, that only an omniscient and omnipotent deity could account for these marvels of mechanical perfection, purpose, and functionality, and for the enormous diversity of inventions that they entail.

Darwin's greatest accomplishment, and his main contribution to the history of ideas, was to show that the complex organization and functionality of living beings can be explained as the result of a natural process, natural selection, without any need to resort to a Creator or other external agent. The origin and adaptation of organisms in their profusion and wondrous variations were thus brought into the realm of science.

3 Natural selection versus evolution

Important as the evidence for evolution was, Darwin considered the discovery of natural selection to be his most important scientific achievement, as becomes apparent from consideration of his life and works. In his diaries and correspondence, Darwin referred to natural selection as 'my theory,' a designation he never used when referring to the evolution of organisms. The discovery of natural selection, Darwin's awareness that it was a greatly significant discovery because it was science's answer to Paley's argument from design, and Darwin's designation of natural selection as 'my theory,' can be traced in Darwin's *Red Notebook* and his *Transmutation Notebooks B to E*, which he started in March 1837, not long after returning (on 2 October 1836) from his five-year voyage on the *Beagle*, and completed inlate 1839 (Eldredge 2005, pp. 71–138).

The evolution of organisms was commonly accepted by naturalists in the middle decades of the nineteenth century. The distribution of exotic species in South America, in the Galápagos Islands, and elsewhere, and the discovery of fossil remains of long-extinguished animals, confirmed the reality of evolution in Darwin's mind. The intellectual challenge was to explain the origin of distinct species of organisms, how new ones are adapted to their environments, that 'mystery of mysteries,' as it had been labeled by Darwin's older contemporary, the prominent scientist and philosopher Sir John Herschel.

Early in the *Notebooks* of 1837–1839, Darwin registers his discovery of natural selection and repeatedly refers to it as 'my theory'. From then until his death in 1882, Darwin's life would be dedicated to substantiating natural selection and its companion postulates, mainly the pervasiveness of hereditary variation and the enormous fertility of organisms, which much surpassed the capacity of available resources. Natural selection became for Darwin 'a theory by which to work'. He relentlessly pursued observations and performed experiments in order to test the theory and resolve presumptive objections.

As I read it, Darwin's focus in *Origin* was the explanation of the adaptations or design of organisms, with evolution playing the subsidiary role of supporting evidence. The introduction and chapters I through VIII explain how natural selection accounts for the adaptations and behaviors of organisms, their 'design'. The extended argument starts in chapter I, where Darwin describes the successful selection of domestic plants and animals and, with considerable detail, the success of pigeon fanciers seeking exotic 'sports'. The success of plant and animal breeders manifests how much selection can accomplish by taking advantage of spontaneous variations that occur in organisms but happen to fit the breeders' objectives. A sport (mutation) that first appears in an individual can be multiplied by selective breeding, so that after a few generations that sport becomes fixed in a breed, or race. The familiar breeds of dogs, cattle, chickens, and food plants have been obtained by this process of selection practiced by people with particular objectives.

The ensuing chapters (II–VIII) of *Origin* extend the argument to variations propagated by natural selection for the benefit of the organisms themselves, rather than by artificial selection of traits desired by humans. As a consequence of natural selection, organisms exhibit adaptive organs and functions. The 'design' of organisms as they exist in nature, however, is not 'intelligent design' imposed by God as a 'Supreme Engineer' or by humans; rather, it is the result of a natural process of selection, promoting the adaptation of organisms to their environments. This is how natural selection works: individuals that have beneficial variations, i.e., variations that improve their probability of survival and reproduction, leave more descendants than individuals of the same species that have less beneficial variations. The beneficial variations will consequently increase in frequency over the generations; less beneficial or harmful variations will be eliminated from the species. Eventually, all or most individuals of the species will have the beneficial features; new features will arise over eons of time.

Darwin argues that hereditary adaptive variations ("variations useful in some way to each being") occasionally appear in organisms, and that these are likely to increase the survival and reproductive chances of their carriers. The success of pigeon fanciers and animal breeders clearly shows the occasional occurrence of useful hereditary variations. In nature, over the generations, Darwin's argument continues, favorable variations will be preserved, multiplied, and conjoined; injurious ones will be eliminated. This is how Darwin summarizes natural selection:

> Can it, then, be thought improbable, seeing that variations useful to man have undoubtedly occurred, that other variations useful in some way to each being in the great and complex battle of life, should sometimes occur in the course of thousands of generations? If such do occur, can we doubt (remembering that many more individuals are born than can possibly survive) that individuals having any advantage, however slight, over others, would have the best chance of surviving and of procreating their kind? On the other hand, we may feel sure that any variation in the least degree injurious would be rigidly destroyed. This preservation of favourable variations and the rejection of injurious

> variations, I call Natural Selection. Variations neither useful nor injurious would not be affected by natural selection (Darwin 1859, pp. 80–81).

It follows from Darwin's explanation of adaptation that evolution must necessarily occur as a consequence of organisms becoming adapted to different environments in different localities, and to the ever-changing conditions of the environment over time, and as hereditary variations become available at a particular time that improve, in that place and at that time, the organisms' chances of survival and reproduction. *Origin*'s evidence for biological evolution is central to Darwin's explanation of design, because this explanation implies that biological evolution occurs, which Darwin therefore seeks to demonstrate in most of the remainder of the book (Darwin 1859, Chaps. IX–XIII).[2]

In the concluding chapter XIV of *Origin*, Darwin returns to the dominant theme of adaptation and design. In an eloquent final paragraph, Darwin asserts the 'grandeur' of his vision:

> It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us. […] Thus, from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely, the production of the higher animals, directly follows. There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, while this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning-endless forms most beautiful and most wonderful have been, and are being, evolved (Darwin 1859, pp. 489–490).

4 Evidence for evolution: the fossil record

Darwin and other nineteenth-century biologists found compelling evidence for biological evolution in the comparative study of living organisms, in their geographic distribution, and in the fossil remains of extinct organisms. Since Darwin's time, the evidence from these sources has become stronger and more comprehensive, while biological disciplines that have emerged recently—genetics, biochemistry, ecology, animal behavior (ethology), neurobiology, and especially molecular biology—have supplied powerful additional evidence and detailed confirmation. Accordingly, evolutionists are no longer concerned with obtaining evidence to support the fact of evolution, but rather are concerned with finding out additional information of the historical process in cases of particular interest.

[2] In the sixth edition of *Origin*, these are chapters X–XIV, and the concluding chapter is XV, because Darwin added one earlier chapter about objections raised against his theory.

Moreover and most importantly, evolutionists nowadays are interested in understanding further and further how the process of evolution occurs.

Nevertheless, important discoveries continue, even in traditional disciplines, such as paleontology. Skeptical contemporaries of Darwin asked about the 'missing links', particularly between apes and humans, but also between major groups of organisms, such as between fish and terrestrial tetrapods or between reptiles and birds. Evolutionists can now affirm that these missing links are no longer missing. The known fossil record has made great strides over the last century and a half. Many fossils intermediate between diverse organisms have been discovered over the years. Two examples are *Archaeopteryx*, an animal intermediate between reptiles and birds, and *Tiktaalik*, intermediate between fishes and tetrapods.

The first *Archaeopteryx* was discovered in Bavaria in 1861, two years after the publication of Darwin's *On the Origin*, a discovery that was noted by Darwin in the last two editions of *On the Origin*. Other *Archaeopteryx* specimens have been discovered in the past hundred years. The most recent, the tenth specimen so far recovered, was described in December 2005. *Archaeopteryx* lived during the Late Jurassic period, about 150 million years ago, and exhibited a mixture of both avian and reptilian traits. All known specimens are small, about the size of a crow, and share many anatomical characteristics with some of the smaller bipedal dinosaurs. Its skeleton is reptile-like, but *Archaeopteryx* had feathers, clearly shown in the fossils, with a skull and a beak like those of a bird. *Archaeopteryx* is now considered an early bird. The recently described *Haplocheirussollers*, fifteen million years older than *Archaeopteryx*, is more nearly intermediate between dinosaurs and birds (Stone 2010; Choiniere et al. 2010).

Paleontologists have known for more than a century that tetrapods (amphibians, reptiles, birds, and mammals) evolved from a particular group of fishes called lobe-finned. Until recently, *Panderichthys* was the known fossil fish closest to the tetrapods. *Panderichthys* was somewhat crocodile shaped and had a pectoral fin skeleton and shoulder girdle intermediate in shape between those of typical lobe-finned fishes and those of tetrapods, which allowed it to 'walk' in shallow waters, but probably not on land. In most features, however, *Panderichthys* was more like a fish than like an amphibious tetrapod. *Panderichthys* is known from Latvia, where it lived some 385 million years ago (the mid-Devonian period).

Until very recently, the earliest tetrapod fossils that are more nearly fishlike were also from the Devonian, about 376 million years old. They have been found in Scotland and Latvia. *Ichthyostega* and *Acanthostega* from Greenland, which lived more recently, about 365 million years ago, are unambiguous walking tetrapods, with limbs that bear digits, although they retain from their fish ancestors such characteristics as true fish tails with fin rays. Thus, the time gap between the most tetrapod-like fish and the most fishlike tetrapods was nearly ten million years, between 385 and 376 million years ago.

Recently several specimens have been discovered of a fossil that has been named *Tiktaalik*, which goes a long way toward breaching this gap; it is the most nearly intermediate between fishes and tetrapods yet known. Several specimens have been found in Late Devonian river sediments, dated about 380 million years ago, on Ellesmere Island in Nunavut, Artic Canada. *Tiktaalik* displays an array of features that are just about as precisely intermediate between fish and tetrapods as one could imagine and exactly fits the time gap as well (Daeschler et al. 2006; Shubin et al. 2006).

The missing link between apes and humans is not, either, missing any longer. The fossils that belong to the human lineage after its separation from the ape lineages are called hominins. Not one, but hundreds of fossil remains from hundreds of individual hominins have been discovered since Darwin's time and continue to be discovered at an accelerated rate. The oldest known fossil hominins are six to seven million years old, come from Africa, and are known as *Sahelanthropus* and *Orrorin*. These ancestors were predominantly bipedal when on the ground and had very small brains. *Ardipithecus* lived about 4.4 million years ago, also in Africa. Numerous fossil remains from diverse African origins are known of *Australopithecus*, a hominin that appeared between three and four million years ago. *Australopithecus* had an upright human stance but a cranial capacity of less than 500 cc, comparable to that of a gorilla or chimpanzee. The skull of *Australopithecus* displayed a mixture of ape and human characteristics. Other early hominins partly contemporaneous with *Australopithecus* include *Kenyanthropus* and *Paranthropus*; both had comparatively small brains. *Paranthropus* represents a side branch of the hominin lineage that became extinct.

Along with increased cranial capacity, other human characteristics have been found in *Homo habilis*, which lived between about two and 1.5 million years ago in Africa and had a cranial capacity of more than 600 cc, and in *Homo erectus*, which evolved in Africa some time before 1.8 million years ago and had a cranial capacity of 800–1,100 cc. Shortly after its emergence in Africa, *H. erectus* spread to Europe and Asia, even as far as the Indonesian archipelago and northern China. *Homo erectus* fossils from Java have been dated at 1.81 and 1.66 million years ago, and from Georgia between 1.6 and 1.8 million years ago.

The transition from *H. erectus* to *H. sapiens* may have started around 400,000 years ago. Some fossils of that time appear to be 'archaic' forms of *H. sapiens*. The species *Homo neanderthalensis* appeared in Europe more than 200,000 years ago and persisted until 30,000 years ago. The Neanderthals have been thought to be ancestral to anatomically modern humans, but comparisons of DNA from Neanderthal fossils with living humans indicate that *H. neanderthalensis* may have been a separate species that became extinct. Another contemporary species, more closely related to Neanderthals than to *H. sapiens*, is known from the Denisova cave in Siberia. This species is known mostly from a small finger bone whose DNA has been sequenced. The members of the species, still unnamed, are referred to as Denisovans (Reich et al. 2010).

5 Molecular evolution

Darwin surely would have been pleased by the enormous accumulation of paleontological evidence, including the discovery of fossils of organisms intermediate between major groups, such as *Archaeopteryx*, *Haplocheirus* and *Tiktaalik*, as well as fossils from diverse species of hominins, intermediate between apes and

Homo sapiens. But there are good reasons to believe that Darwin would have been most pleased and most impressed with the overwhelming evidence for evolution and precise information about evolutionary history provided by molecular biology, a source of evidence and document of history that Darwin could not have even imagined.

Molecular biology, a discipline that emerged in mid-twentieth century, nearly 100 years after the publication of *Origin*, undoubtedly provides the strongest evidence yet of the evolution of organisms. Molecular biology proves evolution in two ways: first, by showing the unity of life in the nature of DNA and the workings of organisms at the level of enzymes and other protein molecules; second, and most important, by making it possible to reconstruct evolutionary relationships that were previously unknown, and to confirm, refine, and time all evolutionary relationships from the universal common ancestor up to all living organisms. The precision with which these events can be reconstructed is one reason why the evidence from molecular biology is so useful to evolutionists and so compelling.

DNA and proteins have been called ‘informational macromolecules’ because they are long linear molecules made up of sequences of units—nucleotides or amino acids—that embody evolutionary information. Comparing the sequence of the components in two macromolecules establishes how many units are different. Because evolution usually occurs by changing one unit at a time, the number of differences is an indication of the recency of common ancestry. Thus, the inferences from paleontology, comparative anatomy, and other disciplines that study evolutionary history can be tested in molecular studies of DNA and proteins by examining the sequences of nucleotides (in DNA) and amino acids (in proteins).The authority of this kind of test is overwhelming: each of the thousands of genes and thousands of proteins contained in an organism provides an independent test of that organism’s evolutionary history.

Molecular evolutionary studies have three notable advantages over comparative anatomy and the other classical disciplines: precision, universality, and multiplicity. First, the information is readily quantifiable. The number of units that are different is easily established when the sequence of units is known for a given macromolecule in different organisms. It is simply a matter of aligning the units (nucleotides or amino acids) between two or more species and counting the differences. The second advantage, universality, is that comparisons can be made between very different sorts of organisms. There is very little that comparative anatomy can say when, for example, organisms as diverse as yeasts, pine trees, and human beings are compared, but there are numerous DNA and protein sequences that can be compared in all three. The third advantage is multiplicity. Each organism possesses thousands of genes and proteins, every one of which reflects the same evolutionary history. If the investigation of one particular gene or protein does not satisfactorily resolve the evolutionary relationship of a set of species, additional genes and proteins can be investigated until the matter has been settled.

The resourcefulness of molecular biology to study evolution can be noted in other ways as well. The widely different rates of evolution of different sets of genes opens up the opportunity for investigating different genes in order to achieve different degrees of resolution in the tree of evolution. Evolutionists rely on slowly evolving genes for reconstructing remote evolutionary events, but increasingly faster evolving genes for reconstructing the evolutionary history of more recently diverged organisms.

Genes that encode ribosomal RNA molecules are among the slowest evolving genes. They have been used to reconstruct the evolutionary relationships among groups of organisms that diverged very long ago: for example, among bacteria, archaea, and eukaryotes (the three major divisions of the living world), which diverged more than two billion years ago, or among the protozoa compared with plants and with animals, groups of organisms that diverged about one billion years ago. Cytochrome *c* evolves slowly, but not as slowly as the ribosomal RNA genes. Thus, it is used to decipher the relationships within large groups of organisms, such as among humans, fishes, and insects. Fast-evolving molecules, such as the fibrinopeptides involved in blood clotting, are appropriate for investigating the evolution of closely related animals—the primates, for example: macaques, chimps and humans.

It is now possible to make an assertion that would have delighted Darwin and would perhaps startle many scientists and most of the general public: Gaps of knowledge in the evolutionary history of living organisms no longer need to exist. Molecular biology has made it possible to reconstruct the 'universal tree of life', the continuity of succession from the original forms of life, ancestral to all living organisms, to every species now living on Earth. The main branches of the tree of life have been reconstructed on the whole and in great detail. More details about more and more branches of the universal tree of life are published in scores of scientific articles every month. The virtually unlimited evolutionary information encoded in the DNA sequence of living organisms allows evolutionists to reconstruct all evolutionary relationships leading to present-day organisms, with as much detail as wanted. Invest the necessary resources (time and laboratory expenses) and one can have the answer toany query, with as much precision as wanted.

Several decades have passed since my first visit to the Stazione Zoologica and more than thirty years since the 1982 symposium to celebrate the 100th anniversary of Darwin's death. With awe I notice how much our knowledge of biological evolution has advanced in the intervening years—such as, for example, the blooming of molecular evolution, the advances of evo-devo, and the discovery of innumerable hominin fossils—and the significant contributions of the Anton Dohrn Stazione to the advances. It is surely pertinent at this time to celebrate Christiane Groeben's lasting accomplishments.

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